

HATCHING SUCCESS AND NEST PREDATION IN THE GREEN SEA TURTLE, *CHELONIA MYDAS*, AT TORTUGUERO, COSTA RICA¹

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Abstract. Green turtle hatching success and nest predation were investigated at Tortuguero, Costa Rica, during July-November 1977.

Forty-two percent of 350 study area nests and 57% of 237 beach survey nests produced emerging young; 38% and 24%, respectively, were destroyed by dogs, coatis, and vultures.

The mean emergence percentage for the successful study area nests was 83%. About 13% of all eggs deposited did not hatch. A mean incubation period of 62 d and a mean clutch size of 104 eggs were recorded.

Emergence success was not influenced by other recorded parameters (nest position on beach, rainfall, turtle's tag year, time of season, incubation period, and clutch size). Incubation period was related to nest position and clutch size.

Dogs, coatis, and black and turkey vultures were the chief predators at Tortuguero; dogs did the most damage. Dogs and coatis found nests at all stages of development, but destroyed more nests containing hatchlings than nests containing unhatched eggs.

Predation was related to nest position, but not to nest density. Nests were destroyed in equal proportion on the entire 35.4 km of beach. Predator activity was not consistent throughout the season; proportionally more nests were destroyed near the end of the nesting season than during the beginning.

Key words: *Chelonia mydas*; clutch size; Costa Rica; dogs; hatching success; incubation period; predation; sea turtles; Tortuguero.

INTRODUCTION

Sea turtles, perhaps because of a growing public awareness of their status as endangered species, increasingly have become the subjects of research. Little is known, however, about the hatching success of sea turtles or the extent of predation on nesting beaches, as few quantitative studies under natural conditions exist that deal with either of these topics.

Hatching success most often is studied under hatchery conditions. Hirth (1971) summarized green turtle (*Chelonia mydas*) hatching success data from areas around the world. Egg translocation, particularly when the eggs are handled carelessly, lowers the percentage of eggs which hatch (Pritchard 1969a, Bustard 1973). Consequently results reported in hatchery studies may not indicate accurately natural survival rates.

Recently Bustard (1973), Schulz (1975) and G. H. Balazs (personal communication) investigated the hatching success of undisturbed natural nests of green turtles in Australia, Surinam, and the northwestern Hawaiian Islands, respectively.

Quantitative information on nest predation is fragmentary. Many authors have discussed the role that heavy predation pressure probably played in the adaptive selection of islands and isolated beaches by sea turtles for nesting (Hendrickson 1958, Bustard 1973, Carr et al. 1974). Most major sea turtle studies also

list known and probable predators of turtle eggs and hatchlings. Hirth (1971) summarized information on egg and hatchling predators for green turtles from different localities, but most of this information is qualitative or anecdotal. Schulz (1975) and Worth and Smith (1976) discussed predation and gave nest-loss percentages for Surinam green turtles and Florida Atlantic Coast loggerheads. Burger (1977) and Davis and Whiting (1977) made thorough studies of the effects of heavy predation on diamondback terrapin (*Malaclemys terrapin*) nests in New Jersey, and on Florida Everglades loggerhead (*Caretta caretta*) nests. Similar studies on green sea turtles are unavailable.

My research involved following undisturbed natural nests from the day eggs were laid until death or emergence of the clutch. Specifically my goals were: (1) to determine the percentage of success in natural emergence for the Tortuguero green turtle, (2) to examine the possible influences of other parameters (rainfall, incubation time, clutch size, time of season, nest position, and turtle tag year) on emergence success, (3) to determine the number of unhatched eggs in each nest, and to examine the embryos within these, (4) to determine mean incubation period and clutch size, and to investigate the relationship between these and other parameters, (5) to compare the nesting success of remigrant turtles and first-time nesters, (6) to investigate the extent, timing, and types of predation; to determine how other parameters influence predation, and (7) to investigate the number of nests lost to human poachers and to beach erosion.

¹ Manuscript received 12 July 1978; accepted 16 February 1979.

THE STUDY AREA

The Tortuguero nesting beach is located on the Caribbean coast of Costa Rica, between Puerto Limon and the Nicaraguan border. This unbroken strip of black sand beach extends 35.4 km from the mouth of Rio Tortuguero south to Rio Parismina. Along its entire length the nesting beach is closely backed by a natural river system.

Since the early 1950's Dr. Archie Carr has directed a project for tagging the sea turtles on the northernmost section of the nesting beach. There the entire beach is divided into .20-km segments with the mouth of Rio Tortuguero designated as kilometre zero. The tagging during the summer of 1977 was confined to the first 8.1 km of beach. The study area for the present research included the southern 4 km (kilometre 4.0 to kilometre 8.1) of the 8.1-km tagging area. In addition, less comprehensive surveys were made from kilometre 8.1 to kilometre 35.4.

Tortuguero beach is constantly subject to alterations resulting from surf erosion and rebuilding. Heavy rains and stormy seas greatly accelerate the normal erosion process. Thus, over a period of only a few days beach contours can vary considerably. Stretches of the beach are heavily littered with branches, logs, and hyacinth rafts from the river mouths.

On most of its length the lower half of the nesting beach is open but littered sand. Above this open expanse grow various low, herbaceous, salt-resistant plants including railroad vine (*Ipomea pes-caprae*), seapurslane (*Sesuvium portulacastrum*), and rush grass (*Sporobolus virginicus*). A border of cocoplum (*Chrysobalanus icaco*) and seagrape (*Coccolobis uvifera*) separates the beach from the coconut palm (*Cocos nucifera*) forest. Hirth (1963) provided a more detailed description of the vegetation.

METHODS

This investigation consisted of two main parts. All nests on the 4-km study area were followed daily and studied carefully. After the young emerged, the nest contents were dug up and examined. In addition, I made longer beach surveys of 17.7 and 35.4 km to obtain a profile of predator activity for the entire nesting beach.

The daily work was coordinated with the tagging project. Each night, from 13 July to 14 September 1977, female turtles that had completed nesting were turned by students and villagers who patrolled the beach from 2000 until 0400. The next morning these turtles were tagged, measured, and released. New body pits (1–2 m in diameter) were marked with a strip of numbered flagging tape tied to a wooden stake.

Data recorded for each nest included its location and position on the beach platform (see Fig. 1), and the tag number of the mother turtle.

Maps were made to facilitate relocating nests, and

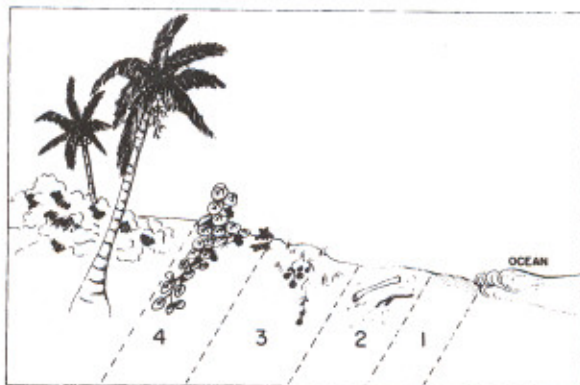


FIG. 1. Nest position on beach profile: #1 = Low on beach, washed by surf; #2 = Mid-beach, open sand and debris; #3 = At vegetation line, in sparse railroad vine and grass; #4 = In vegetation (cocoplum and seagrape).

vegetational cover was noted and described. In addition, daily rainfall records were kept for July through November.

Each morning through 15 September, new nests were marked and existing nests were checked for disturbance by predators, surf, other turtles, or man. Although I marked no additional nests after 15 September, old nests were checked daily until 19 November by which time all hatchlings had emerged or been taken by predators.

In mid-November a systematic search was begun for eggs that were past their hatching date. By poking around the body pit with a thin stick, several clutches from which hatchlings had emerged unseen and a few with dead, unhatched eggs or dead hatchlings were found.

Hatchlings usually emerge at night. The following morning I determined the number of empty egg shells, unhatched eggs, and dead and living hatchlings remaining in the egg chamber. Unhatched eggs were opened and examined for signs of development. If they contained embryos, these were measured and checked for deformation. Hatchling position in the chamber column was recorded, and hatchlings were examined for deformities. Any predator disturbance at emergence was noted. Finally, if numbers of hatchlings were small, their tracks to the sea were counted.

The accuracy of the egg counts varied, depending upon the condition of the nest contents. In some nests empty shells were undamaged except for the hatchling's exit; in others, shells were torn and fragmented. To measure egg-counting accuracy I counted the shells in several emerged hatchery nests of known clutch size. My error in several trials ranged from ± 8 eggs in a large clutch of 164 torn eggs to ± 0 .

Beach surveys were made every Saturday during the tagging season and, with two exceptions, each Saturday thereafter until 18 November. Fresh nests were

TABLE 1. Fates of marked study area nests (kilometre 4.0 to kilometre 8.1).

Nest fate	Number	Percent of active nests
Undisturbed, young emerged	148*	42.6
Disturbed, some young emerged	18	4.9
Destroyed by animal predator	122	34.8
Dead although undisturbed	19	5.4
Washed out by surf	20	5.7
Lost to human predators	23	6.6
Total active nest sites	350	100.0
Undetermined fate	86	—
False nest	14	—
Total other nest sites	100	—
Total nest sites	450	—

* This includes 134 nests for which complete data were obtained, nine nests for which natural emergence success was not obtained, three nests I dug up before they emerged, and two nests that emerged unseen for which no original clutch size could be estimated.

marked with a numbered flagged stake, and vegetation, mileage, and beach position were recorded. On subsequent surveys existing marked nests were checked for predator disturbance and wave-washing, until loss or emergence of young. I made 17.7- and 35.4-km surveys on alternate weeks through 9 September. From 16 September until 18 November only 17.7-km surveys were made.

Because too much time was required to mark all fresh nests on 35.4-km surveys, only nests on the last 17.7 km were marked after 6 August. As a result, nests on the first 17.7 km of the nesting beach were checked weekly until 16 September and fresh nests were marked every other week until 6 August; nests on the last 17.7 km were checked and marked every 2 wk until 16 September.

The data collected from the study area and the beach surveys were analyzed using nonparametric statistical tests (Siegel 1956). The rejection level for the null hypothesis in all statistical tests was $\alpha = .05$. Although complete data were unobtainable for some of the nests, they were included in the analyses whenever possible.

RESULTS

Fates of study area nests

The fates of 350 of the 450 marked study area nest sites were determined (Table 1). Of the nests on the study area beach 42.6% were undisturbed during their incubation and successfully produced emerging young. Another 39.7% of the nests were completely destroyed, or disturbed and partially destroyed by dogs (*Canis familiaris*), coatis (*Nasua narica*), and black and turkey vultures (*Coragyps atratus*, *Cathartes aura*). Although not disturbed by animal predators,

TABLE 2. Date, length, and number of nests marked on 17 beach surveys.

Date survey made	Length of survey (kilometres)	Number of nests marked
July 15	35	35
July 22	18	21
July 29	35	26
August 6	18	94
August 12	35	34
August 19	18	85
August 26	35	39
September 2	18	123
September 9	35	1
September 16 through November 18 (eight surveys)	18	—

man, or surf, the entire clutch in 5.4% of the nests failed to hatch. Beach erosion destroyed 5.7% of the active nests and human poachers took the remaining 6.6%.

The fates of 86 marked nest sites remained undetermined. After waiting considerably longer than the normal incubation period, I could not locate eggs in these nests by searching with a thin stick. As there was no positive proof that these were active nests (i.e., they may have been false nesting attempts, the eggs may have been infertile, or the embryos may have died), these nests have been dropped from further analysis. An additional 14 marked nest sites were known to be false nesting attempts. In these instances, turtles that appeared to have nested were turned, tagged, and released, only to return to nest within the next few days. False nests also have been eliminated from the analysis. It was difficult to identify individually 29 other nests where two or more turtles laid eggs in the same body pit. Likewise it was impossible to distinguish hatchlings when they began emerging or were lost to predators. Data from combined nests were included in the analysis only when emergence date or the turtle's tag number was not crucial.

Fates of beach survey nests

On 17 beach surveys, made July to November 1977, 458 nest sites were marked (Table 2). Hatchlings emerged from 55.7% of the 237 nests that I followed to completion of incubation (Table 3). Animal predators destroyed 24.5%, beach erosion 16%, and human poachers 2%. These values are comparable to those obtained from the study area data (Table 1). However, the number of beach survey nests for which fates were not determined was more than twice the number of those in the study area. Undoubtedly the less frequent checking of beach survey nests caused this discrepancy.

TABLE 3. Fates of marked beach survey nests (kilometre 8.1 to 35.4).

Nest fate	Number	Percent of active nests
Young emerged	132	55.7
Disturbed by predators, some young emerged	3	1.3
Destroyed by animal predator	58	24.5
Washed out by surf	39	16.4
Lost to human poachers	5	2.1
Total active nest sites	237	100.0
Lost (18- and 35-km survey)	129	—
Undetermined fate (18-km survey)	47	—
Not followed to completion (35-km survey)	45	—
Total other nest sites	221	—
Total nest sites	458	—

At some time during incubation the stakes that marked 129 nests were knocked over, and on subsequent surveys these nests could not be relocated. Although 47 other nests were followed longer than the normal incubation period, they were never disturbed by predators nor were any hatchlings seen to emerge. Another 45 nests, all located on kilometres 17.7 to 35.4 were not followed to completion because 35.4-km surveys were not made after 9 September. These 221 nests with undetermined fates were omitted from all statistical analyses.

Hatching and emergence success of study area nests

Undisturbed study area nests that produced young were examined thoroughly. I determined the percentage of young successfully emerging from each nest by subtracting the number of hatchlings left in the nest column from the number of empty shells and dividing

this difference by the total clutch size. The sum of the number of unhatched eggs and empty shells removed from a nest was used as an approximation of total clutch size.

The mean percent emergence success for the 134 successful, undisturbed study area nests examined was 83.1%. In this calculation only nests that produced young were considered; nests with eggs that failed to hatch (5.4%, see Table 1) were not included.

Table 4 shows an analysis of the fates of 14 272 eggs examined from the 134 undisturbed nests. A total of 11 813 eggs produced young that successfully emerged. The young from 461 eggs hatched but did not emerge, and were found in the nest column when the nests were dug up the morning following emergence. Live hatchlings found deep in the egg column, alone or in small numbers, were doomed, as they would not be able to work their way up to the surface and emerge. In addition to these "normal" young, 21 deformed hatchlings were found in 11 nests. Abnormalities of flipper and carapace were the most common deformities observed.

Another 1977 eggs (13.8% of total) were unhatched, containing embryos or being infertile. While 63.9% of the active nests contained eggs with unhatched "normal" embryos, over 92% contained infertile eggs. Deformed embryos were found in eggs in 11% of the nests. Abnormal scute patterns and embryos curled backward instead of around the yolk sac were among the common deformities. One two-headed embryo near hatching size (3.8 cm in length) was found.

To test for a relationship between emergence success and nest position on the beach, a Kruskal-Wallis one-way analysis of variance was performed on the study area data. The amount of rainfall during the incubation period and the emergence success of a nest were compared, using a Spearman rank correlation. Emergence success was not related to either nest position or amount of rainfall.

TABLE 4. Fates of eggs in 134 study area nests.

Egg fate	Number of eggs	Percent of total eggs	Number of nests	Percent of nests
Hatched				
Emerged	11 813	82.77	134	100
Dead "normal" left in nest	323	2.26	39	28.68
Live "normal" left in nest	138	.97	25	18.38
Deformed left in nest	21	.15	11	8.09
Total	12 295*			
Unhatched				
Infertile/undeveloped	1258	8.81	126	92.65
"Normal" embryo	671	4.70	87	63.97
Deformed embryo	40	.28	15	11.03
Albino	5	.04	5	3.68
Twins	3	.02	3	2.21
Total	1977*			

* 14 272 total eggs examined.

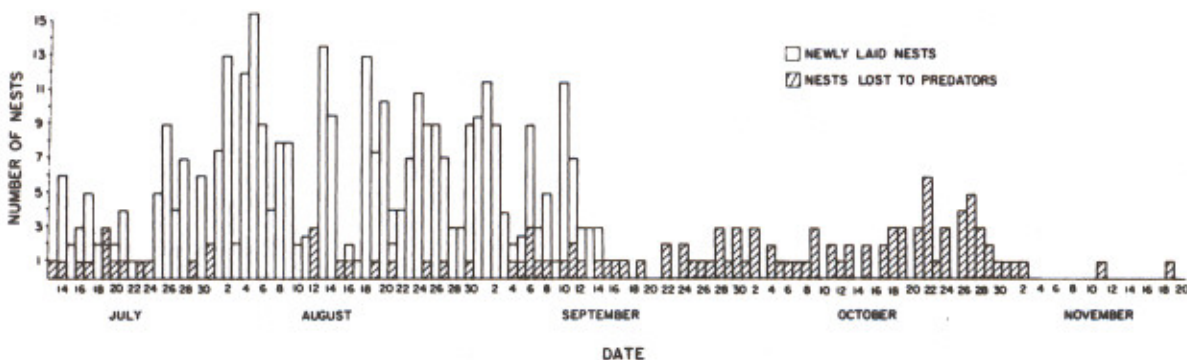


FIG. 2. Nightly variation in nesting and predation during the nesting season in 1977.

Nesting turtles were classified according to nesting "age," i.e., according to the number of years since they had been tagged. Using a Mann-Whitney U test, the emergence success of 100 nests of "old" turtles (turtles tagged in 1965–1976 plus those with missing tags) was compared with the success of 212 nests of first-time nesters. There was no significant difference between the emergence success of clutches laid by these two groups. Chi-square tests were used to investigate a possible relationship between tag year and abnormalities of young or number of unhatched and infertile eggs. No significant difference between the two groups was found.

The nesting season at Tortuguero began in June and peak nesting activity occurred in early August (Fig. 2). By late November only a few turtles were still nesting. The tagging project, and consequently this research, dealt only with turtles that nested during the middle two months of the season (13 July–14 September). Dividing these months into four consecutive 2-wk segments allowed a Kruskal-Wallis analysis of variance to be used to test for a seasonal difference in emergence success. No relationship was found between the date of nesting and emergence success.

Finally, comparisons were made between emergence success and three additional parameters. Length

of incubation (Kruskal-Wallis analysis of variance), clutch size (Spearman rank correlation), and the successive clutches of a turtle (Wilcoxon signed-ranks test) were not correlated with emergence success.

Incubation period and clutch size of study area nests

A mean incubation period of 61.9 d was determined using the lengths of incubation from 125 undisturbed study area nests. For the purpose of this report, "incubation period" is the length of time the eggs incubate plus the time for the hatchlings to emerge from the nest. Fig. 3 shows the frequency distribution of these incubation periods. Incubation periods ranged from 53 to 81 d, with a standard deviation of 5.13 d.

Nest position and incubation period were compared using a Kruskal-Wallis analysis of variance, and were found to be related ($H = 11.70$, $df = 2$, $P < .01$). Further comparisons (Mann-Whitney U test) showed significant differences in incubation period between nests on beach positions #1–#2 (low and mid-beach), and #4 (in vegetation) ($z = -3.54$, $P < .001$); and between nests on position #3 (at vegetation) and #4 (in vegetation) ($z = -2.95$, $P < .01$). As shown in Table 5, low and mid-beach nests had shorter incubation periods than nests in the beach border vegetation. However, no significant difference in the length of incubation was found between nests on positions #1–#2 and #3.

Three separate Spearman rank correlation tests were used to compare incubation period and rainfall. Nests at each beach position were analyzed separately to eliminate the effects of nest position on incubation length. No correlation was found between length of incubation and the amount of rainfall during the incubation period.

Spearman rank correlation tests, with nest position effect removed, also were used to investigate any relationship between incubation period and clutch size. Nests on positions #1–#2 and position #3 showed a correlation between incubation period and clutch size ($r = 2.64$, $df = 30$, $P < .2$; $r = 2.22$, $df = 33$, $P < .05$). At these nest positions, as clutch size increased

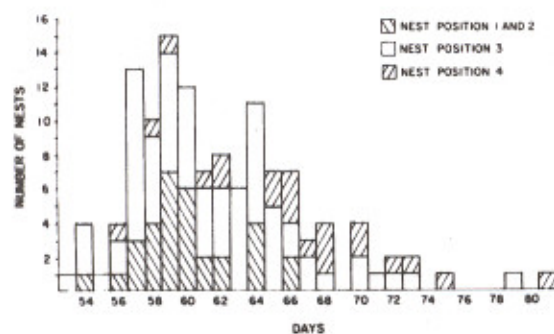


FIG. 3. Distribution of incubation periods with the positions of nests on the beach profile: kilometre 4.0 to 8.1.

TABLE 5. Distribution of nests on beach profile and their mean incubation periods.

Nest position	Description	Number of nests (percent of total nests)	Mean incubation time in days
1 & 2	Low and mid-beach	32 (25)	60.0
3	At dense vegetation	72 (58)	62.4
4	In dense vegetation	21 (17)	66.6
Total		125	

the length of incubation decreased. Position #4 nests showed no such correlation.

A Kruskal-Wallis analysis of variance, with four consecutive 2-wk periods equal to the different treatments, was used to test the study area data for a relationship between length of incubation and date of nesting. No relationship was found.

Distribution of clutch size is illustrated in Fig. 4. All nests for which the original clutch size had been estimated, including some predator-disturbed or destroyed nests, were used to determine the overall mean clutch size of 104.1 eggs. The number of eggs in a clutch ranged from 7 to 178. No split clutches (i.e., incomplete nests; the turtle returns within a night or two to finish laying elsewhere) were observed.

When possible, the number of eggs in the successive clutches of a single turtle was counted and compared. A Wilcoxon signed-ranks test showed no significant difference between the number of eggs in early and late clutches. A turtle's tag year and clutch size also were unrelated. A Kruskal-Wallis analysis of variance was performed on clutch size data for nests from four consecutive 2-wk segments of the nesting season ($H = 20.99$, $df = 3$, $P < .001$); clutch size and the time of season when the eggs were laid were related (see Table 6). Mann-Whitney U tests then were used to determine during which 2-wk intervals of the season clutch sizes were different from one another. Only the two middle periods, 27 July–9 August and 10–23 August, had no significant difference between their average clutch sizes.

Lastly, clutch size and nest positions were tested using a Kruskal-Wallis analysis of variance, and no relationship between these two variables was found.

TABLE 6. Seasonal variation in average clutch size of 130 study area nests.

Time in season (2-wk segments)	Number of nests	Mean clutch size
July 13–26	12	85.2
July 27–August 9	45	102.1
August 10–23	32	103.8
August 24–September 6	41	112.4
Total	130	

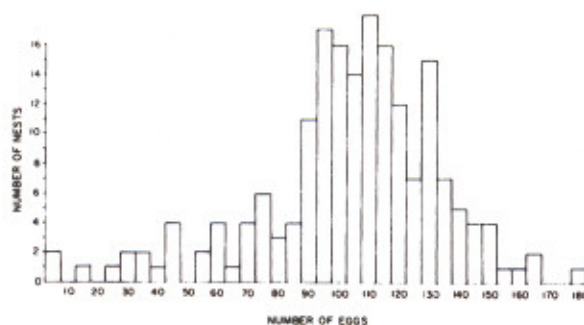


FIG. 4. Frequency distribution of clutch sizes for 188 nests from study area.

Predation

Nest predators (dogs, coatis, and turkey and black vultures) destroyed 34.9% of the active study area nests and 24.5% of the nests sampled by the beach survey method (Table 7).

Dogs, man-introduced predators feeding mostly at night, were responsible for the greatest nest destruction. Coatis, natural, diurnal predators, destroyed far fewer nests than did dogs. An exact estimate of nest damage by coatis was not obtained in this study since they rarely ate all of the eggs in a nest. Evidence of coati disturbance was often obliterated by dogs and vultures that later ate the remaining eggs or young.

Vultures were not seen to dig up nests. They appeared to feed on what coatis and dogs left, and on young turtles that emerged during the day. Coatis feeding on eggs or young sea turtles almost always were surrounded by a ring of vultures. Vultures are efficient predators on emerging young. Headless, flipperless hatchlings strewn on the beach were found near two study area nests from which young had emerged during the daylight hours (Table 7).

Chi-square tests were used to compare the expected and observed number of nests destroyed by predators

TABLE 7. Number of nests destroyed by predators in study area and beach survey area.

Predators	Number of study area nests	Number of beach survey nests*
Dogs	50	13
Dogs and vultures	49	15
Dogs, coatis, and vultures	3	—
Coatis	2	5
Coatis and dogs	4	—
Coatis and vultures	2	2
Vultures (day emergence)	2	—
Unspecified	12	23
Total	124	58

* Due to infrequent checking, these may be less accurate.

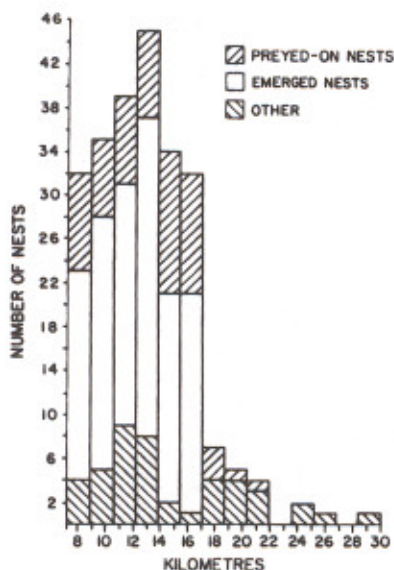


FIG. 5. Number of marked nests on each kilometre of beach survey (kilometre 8.1 to 35.4) with corresponding fates. "Other" includes nests taken by human poachers and nests lost to beach erosion.

on different nest positions for the study area and the beach survey. A highly significant difference was found between the observed and expected values ($\chi^2 = 11.86$, $df = 2$, $P < .01$; $\chi^2 = 13.41$, $df = 2$, $P < .01$). Fewer nests than expected were taken by predators from the low and mid-beach position (#1 and #2). Conversely, nests on position #3 and in particular those on position #4 were destroyed more often than expected. Coatis never opened nests on the low or mid-beach area. They raided only those nests at the vegetation line (position #3) or in the seagrapes and cocoplums (position #4).

Dogs and coatis roamed the entire 35.4 kilometres of the Tortuguero beach. A Spearman rank correlation showed no relationship between the distance from the village and the number of nests destroyed by predators. Further, a chi-square test showed no significant difference between the observed and expected number of predator-destroyed nests on each .80 km of the study area or each 1.61 km of the entire beach. Likewise no correlation exists between predation and the density of nests. Figure 5 shows the number of marked nests on each kilometre of the beach survey area and their fates. Many unmarked nests were successful. For all areas, young emerged successfully from nests and nests were preyed upon approximately in proportion to the total number of nests present.

Predation was not constant throughout the nesting season (Fig. 2). More beach survey nests than expected were raided during the beginning (July) and end (September) of the tagging/nesting season ($\chi^2 = 13.61$, $df = 2$, $P < .01$). Data from the study area showed

more nests than expected destroyed during the last half of August and during September ($\chi^2 = 16.36$, $df = 3$, $P < .001$).

Finally, a Kolmogorov-Smirnov one-sample test was used to see if the frequency of predation varied during the period of incubation. For this test only the 1st 6 wk of incubation in a nest were analyzed, to eliminate the facilitation of predation which occurs once the young hatch and begin moving to the surface. To minimize the effect that time of season might have on predation rate, the nests were grouped in nine cohorts (clutches laid in a 1-wk period), and these were analyzed separately. Nests laid during the 1st wk of the season were differentially preyed upon over their incubation period ($D = 0.527$, $n = 10$, $P < .01$). Frequency of predation was greatest during the week following initiation in this first cohort. In the remainder of the cohorts, nests were disturbed by predators equally throughout their incubation period. Analyses of entire incubation and emergence periods demonstrated that in several of the cohorts the number of destroyed nests that contained hatched young (6th–9th wk of incubation) was significantly greater than the number of newly laid nests destroyed ($P < .05$).

Crabs, ants, maggots, and mites feed on sea turtle eggs and young. Quantitative measure of the damages done by each was not obtained in this study. Ghost crabs, *Ocypode quadrata*, tunneled into at least 13 nests; in one nest, 21 eggs were eaten. The larger crabs also captured emerging young. Ants invaded 35 nests and fed on the remaining hatchlings. They also were found feeding on undeveloped and unhatched eggs. I could not tell whether the ants killed developing eggs and hatchlings, or fed only on dead and weak individuals. Maggots, larvae of the fly *Megaselia scalaris*, were found in great numbers in 50 rotten clutches and nests from which the young had emerged. Mites of the genus *Caloglyphus* were found feeding on dead hatchlings and rotten eggs in 21 nests.

Occasionally a nesting turtle digs into a previous nest site, breaking eggs as she digs. This occurred in five instances on the study area. These turtle-disturbed nests did not produce young; they were invaded by maggots, ants, crabs, and other predators. Natural nest losses to crabs, ants, and other turtles were minimal when compared to losses to dogs.

DISCUSSION

Nesting success

Green turtle reproductive behavior has been monitored at Tortuguero for 22 yr (Carr et al. 1978). Until the 1977 tagging season little research had been done on hatching success and the extent of nest predation.

A mean natural emergence success of 83.1% was recorded for Tortuguero in 1977. This percentage exceeds some hatchery emergence success results for green turtles by 20 to 36%: 47% (Hendrickson 1958),

50–54% (Carr and Hirth 1962), 52–67% (Bustard 1973), and 58.7% (Worth and Smith 1976). My results agree more closely with the natural nest emergence success of 71%, 80%, and 85% reported by Bustard (1973), G. H. Balazs (*personal communication*), and Schulz (1975), respectively.

Emergence success was not correlated with any other variable measured in this study. Some researchers (e.g., Bustard 1973) have claimed that wet weather and/or its associated temperature decrease can lower emergence success. However, no relationship between rainfall and emergence success was noted at Tortuguero. Preliminary findings by G. H. Balazs (*personal communication*) indicate a possible correlation between date of egg deposition and emergence success. Again, no such correlation was found in this study.

Incubation time appeared to be influenced by nest position. Eggs in nests on the open beach had shorter incubation periods than those in nests located near or in the beach border vegetation. This difference probably was due to small temperature variations between nests exposed to full sunlight and those shaded by vegetation. The two study area nests with the longest incubation periods, 79 and 81 d, were shaded completely by trees and seagrass. The finding of Bustard and Greenham (1968) that small changes in temperature have a direct effect on length of incubation under laboratory conditions agrees with these field observations. In their experiment (small sample size used), a three-degree increase in temperature reduced incubation time by 25 d.

Bustard and Greenham (1968) also reported an increase of six degrees in nest temperature during laboratory incubation due to metabolic heating of the eggs. Carr and Hirth (1961) measured an average gain of two to three degrees in natural nests at Ascension Island. Thus, egg mass size (number of eggs) may influence nest temperature and incubation time. Results of my research indicate that incubation length is affected by clutch size. However, the relationship between clutch size and incubation is not straightforward, as only nests on positions #1–#2 and #3 showed the effect. The effects of a temperature increase due to metabolic heating in nests at position #4 (in vegetation) may have been overshadowed by the cooling effect of the vegetation.

Hendrickson (1958) proposed that the size of an egg mass might influence hatching success. Small clutches would be too cool for normal development. Yet, some of the smallest clutches at Tortuguero exhibited hatching successes of 70–80%. In leatherbacks (*Dermochelys coriacea*), Balasingham (1967) found that smaller clutch sizes apparently increased the percent hatchling survival.

The recorded mean incubation period of 61.9 d was slightly longer than means from other studies (Hirth 1971). Hendrickson (1958) reported that the incubation

time of nests in Malaya and Sarawak varies over the nesting season, depending on seasonal changes in environmental conditions (monsoon rainfall and lowered temperature). Though this may occur at some nesting beaches, incubation time did not vary during the 1977 nesting season at Tortuguero, nor was it related to the amount of rainfall.

Clutch size did show seasonal variation in my study. The number of eggs per nest increased as the season progressed. These findings are contrary to those reported by Davis and Whiting (1977) for loggerheads in Everglades National Park, Florida, where mean clutch size decreased during the season. Balasingham (1967) working with leatherbacks and Hendrickson (1958) working with green turtles of Malaya and Sarawak observed no change in mean clutch size throughout the nesting season.

Balasingham (1967) and Hirth (1971) suggested that reproductive capacity of sea turtles may decrease with age. In this study, however, turtle tag year (a crude estimation of relative reproductive age) and emergence success, clutch size, frequency of deformed embryos and young, and frequency of infertile eggs were not related. All five undeveloped or infertile clutches found on the study area were of first-time nesters. This may indicate that newly mature turtles initially are less productive than the older females, but before conclusions can be made concerning age and reproductive capacities, basic information must be obtained about turtle life-spans and the number of years required to reach maturity.

Nest destruction

In 1977 more than half of the green turtle nests on Tortuguero beach were destroyed during incubation. High losses to predators have been noted on other sea turtle nesting beaches around the world. In the United States, raccoons (*Procyon lotor*) destroy as much as 40–80% of the loggerhead and green turtle nests laid on certain beaches (Worth and Smith 1976, Davis and Whiting 1977). Predation on several green turtle beaches in the Galápagos by feral hogs (*Sus scrofa*) and a scarab beetle (*Trox suberosus*) has resulted in emergence successes as low as 36% (Derek Green, *personal communication*). Coyotes (*Canis latrans*) which descend on Ridley (*Lepidochelys kempi*) arribadas at Rancho Nuevo, Mexico (Pritchard 1969b) are yet another example of heavy predation. Still, some nesting areas are relatively predator-free (e.g., Hawaii, G. H. Balazs, *personal communication*).

Dogs at Tortuguero were the greatest threat; on no other nesting beaches reported in the literature are dogs so great a menace. The dog population of the village was between 15 and 20 animals. Only four or five of these were kept tied during the nesting season, although National Park rules require that all dogs be kept off the beach from June through December. Feral dogs are said to converge on the beach from inland

during peak nesting months. This rumor was not substantiated, but nests were destroyed on all 35.4 km of beach and the amount of damage by dogs during the summer and fall of 1977 could scarcely have been done by the village animals alone.

Historically predator pressures may have been very different. The heavy predation by dogs is probably a recent development. Dogs were introduced to the area by man very recently in the green turtle's history, and thus had little importance in shaping its evolution. Before their introduction Tortuguero beach was probably much more predator-free, though in the absence of dogs, coatis may have destroyed more eggs and young. Because this nesting beach is actually an island, completely cut off from the mainland by rivers, it is relatively inaccessible to terrestrial predators. This condition probably has aided in establishing and maintaining the Tortuguero beach as an important nesting area.

A program of dog control has begun at Tortuguero National Park but it is not yet effective. This is the last major nesting area of the green turtle in the western Caribbean, and it should be preserved. Effective dog control would be an important step in increasing and maintaining turtle production on this beach.

Predation was related to nest position on the beach. Nests in or near seagrass and cocoplum were destroyed more often by predators than those on low or mid-beach positions. Conversely, beach erosion affected nests only near the surf line. These two opposing pressures may favor nesting in the mid-beach, away from areas of both heavy predation and beach erosion. Many more immediate factors play a role in nest site selection (sand moisture, beach topography, presence or absence of roots, etc.; Bustard 1973). Turtles that nested more than once in 1977 did not consistently choose the same nest position. This finding implies that the immediate environmental factors encountered may have a greater influence on nest site selection than do predation and beach erosion.

S. Stancyk, O. Talbert, and T. McKee (*personal communication*) determined that 37% (June), 45% (July), and 93% (August) of the marine turtle nests on Cape Island, South Carolina, were raided on the night eggs were laid. Burger (1977) found that mammalian predators dug up terrapin nests in New Jersey the night after laying. Her data revealed a second peak of predation at hatching time. A common belief of many sea turtle researchers has been that predation level decreases as the visual and olfactory signs of a nest fade during the season.

At Tortuguero, dogs and coatis found nests at all times during incubation. Moreover, throughout the season, with the exception of the 1st wk, nests at all stages of the 6-wk prehatching period were disturbed with equal frequency. Many nests laid the 1st wk of the season were destroyed almost immediately. At this time there were, of course, no older nests available.

Later in the season there was a noticeable shift in predator preference. As nests reached hatching time and the young began moving towards the surface, predators destroyed a proportionally larger number of the older nests. Thus, analysis of the entire 9 wk of incubation/emergence time indicated that statistically more nests were destroyed during October and November, in the 7th, 8th, and 9th wk of their incubation than earlier. This information, coupled with results (see page 952) showing that predation was not at a consistent level throughout the season, supports the following synopsis.

Early in the nesting season, many nests were destroyed in the first days following their construction. As the season progressed, though visual and olfactory signs of the nests faded, nests of all ages were destroyed in more equal proportions. Once nests began to reach hatching age, however, they were apparently preferred by predators. Whether this apparent preference is related to the ease of finding a nest is not known.

Vultures are opportunistic predators on sea turtle eggs and hatchlings, and are particularly destructive of young that emerge during the day. The temperature-sensitive mechanism whereby most hatchlings emerge during the dark hours no doubt has great survival value (Hendrickson 1958, Carr and Hirth 1961, Bustard 1967).

Ghost crabs have been reported to eat turtle eggs and young at nesting beaches around the world. Hirth and Carr (1970) mentioned crabs as predators on western Indian Ocean islands. Hendrickson (1958) and Hughes (1974) reported crabs eating young and eggs on Malayan and southeast African beaches. Hill and Green (1971) found in Surinam that crabs tunneled into green turtle nests and typically destroyed 11.8% of the eggs. Approximately 60% of all nests were attacked by crabs within 4 d of laying.

Crab destruction was not monitored carefully at Tortuguero, as this would have required excavation of nests before the hatchlings emerged and would have affected the primary research. Crab burrows were found in at least 13 nests.

The larvae of *Megaselia scalaris* probably feed on dead and weakened hatchlings unable to emerge. Little is known of the life history of these flies but it has been suggested that they deposit their eggs as the female turtle is laying (G. Steyskal, *personal communication*). Ants also feed on the weakened young. In addition they chew into eggs, particularly those in vegetated areas. Egg destruction by ants has been recorded in various terrestrial and freshwater turtle species (Burger 1977).

Turtle activity on areas of high nest density may destroy previously laid clutches. Beach erosion results in additional egg losses. Because turtle nesting in 1977 was slack and the sea was unusually calm, neither of these was an important factor during this study.

Poaching by humans also was not a major problem. The National Park guards arrested three poachers early in the season, and this seemed to discourage others.

Despite the heavy predation, approximately 50% of the eggs laid on Tortuguero beach produce hatchlings that reach the water. In order to maintain a stable population of course, a female need only produce two offspring that eventually reproduce. Estimating from past records, each female that nests on the Tortuguero beach lays several thousand eggs, perhaps as many as 10 000 or more, during her reproductive lifetime. Offshore predation on hatchlings by sharks and other predatory fishes, and by predatory birds such as frigate birds and gulls, obviously must be very heavy. Thus predation by dogs may have only a minor effect on turtle recruitment. In fact, dogs may now simply be taking some of the hatchlings that have historically been taken by offshore predators. In order to fully understand the population dynamics of the green turtle the extent of predation on hatchlings and yearlings needs further investigation.

ACKNOWLEDGMENTS

I would like to thank Dr. John H. Kaufmann and Dr. Archie F. Carr for their guidance during this study and their review of the manuscript. I am grateful to Karen Bjorndal, Steve Carr, Matt Dickinson, and the other 1977 Tortuguero turtle-turners for their help in the field. I would also like to thank John Roe and Cliff Abraham for their review of the manuscript, and Peter Feinsinger for his help with the statistics. This research was supported by National Science Foundation grant OCE77-09842 and the Caribbean Conservation Corporation.

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